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Short communication

Suckling and allosuckling behavior in wild giraffe (*Giraffa camelopardalis tippelskirchi*)

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ABSTRACT

Allosuckling has been reported in many mammalian species. In giraffe, allosuckling has been observed in captivity, and the milk theft hypothesis with reciprocity is regarded as the likeliest explanation for this behavior. However, reports of such behavior in the wild remain sparse to non-existent. Here, we studied the suckling and allosuckling behaviors of three nursing giraffe and their offspring (two calves and one juvenile) for 32 days in the Katavi National Park, Tanzania. In total, we observed 56 suckling bouts, 96 suckling attempts, 5 allosuckling bouts, and 71 allosuckling attempts. We observed that the female decided when to nurse the offspring, as reported in previous studies; however, the suckling bouts of calves were terminated mainly by other individuals. On the other hand, all suckling bouts of juvenile were terminated by the female. The milk theft hypothesis was supported since (1) the allosuckler always joined a suckling pair and never succeeded when approaching a female by itself, (2) the female apparently did not notice the non-filial offspring positioned behind the filial offspring, and (3) the female showed active signs of rejection when she noticed the allosuckler. In addition, we found that juvenile close to weaning showed the highest rate of allosuckling interactions. Therefore, we assume that the presence of a weaning individual might drive the occurrence of allosuckling in giraffe in the wild.

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Lactation incurs a high energy cost to females (Martin, 1984). However, females sometimes nurse a non-filial offspring, i.e., an allosuckler (Packer et al., 1992). This behavior is called allosuckling or allonursing, and it is considered as an extreme case of alloparental care in mammals (Riedman, 1982). Allosuckling has been reported in many ungulate species both in captivity and in the wild; examples of the former include Plains zebra (*Equus burchellii*; Pluháček et al., 2011) and guanaco (*Lama guanicoe*; Zapata et al., 2009a), and for the latter, Cape mountain zebra (*E. zebra zebra*; Penzhorn, 1984) and Guanaco (Zapata et al., 2009b). Several hypotheses have been proposed to explain this phenomenon as either adaptive or non-adaptive for nursing females: kin selection, when the involved female and non-filial offspring share genes by common descent (Packer et al., 1992); parenting, so females can improve their maternal skills (Roulin, 2002); reciprocity, wherein two involved females achieve a higher fitness when nursing each other's offspring to a similar extent than when they do not share milk (Packer et al., 1992); misdirected parental care, the inadvertent transfer of milk to nonrelated offspring (Packer et al., 1992); milk evacuation, a female releases surplus milk that her own offspring did not consume (Roulin, 2002); social benefits, allonursing females gain stronger social bonds (Baldovino and Di Bitetti, 2008) and milk theft, the suckling by non-filial calves, usually with the filial calf rather than alone (Brandlová et al., 2013; Glonehová et al., 2016, 2017; Packer et al., 1992) and with non-filial offspring suckling from the lateral position (Brandlová et al., 2013). In addition, MacLeod and Lukas (2014) found that allonursing occurs more often when the cost of allonursing an additional offspring is low.

Giraffe (*Giraffa camelopardalis*) are reported to allosuckle when they are in captivity (Gloneková et al., 2016, 2017) and also in the wild (Pratt and Anderson, 1979). In captivity, allosuckling occurred at the highest rate among mammals. The non-filial calves more often allosuckled together with the filial ones than alone and tried to adopt positions where they may be harder to recognize and this supported the "milk theft" hypothesis as well as the reciprocity (Gloneková et al., 2016, 2017). In contrast, Pratt and Anderson (1979) recorded only one case of allosuckling out of 37 suckling attempts, and Gloneková et al. (2017) recorded no allosuckling event while observing giraffe in a nature reserve for 22 days. These results prompted them to conclude that female giraffe in the wild nurse only filial offspring.

Here, we report in detail the occurrence of suckling and allosuckling behavior in wild giraffe (*G. c. tippelskirchi*) and document

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the conditions of suckling which may influence the occurrence of allosuckling. Even though our sample size was limited to three female-offspring dyads, we also discuss the behavioral evidence for the parenting, reciprocity, misdirected parental care, milk evacuation, social benefits, and milk theft hypothesis.

Our study was conducted from October through November 2017 in Katavi National Park, Tanzania, in which miombo woodlands form the major vegetation (Waltert et al., 2008). We collected data from approximately 07:00–18:00. We conducted our study on foot with an armed ranger. In the park where our study was conducted, the living quarters of the park staff were located near our study area, and the staff normally walked around on foot. Therefore, the giraffe living in this area were more habituated to people than those living outside of this area. Typically, the distance between the observer (M.S.) and animals was 15–50 m, depending on the vegetation and terrain. Since Leuthold (1979) and Pratt and Anderson (1979) noted that nursing females often have their calf within 200-m, all individuals within approximately this area were presumed to belong to the same herd. The estimated age of all individuals were grouped as follows: (1) Calf: <6 months. (2) Juvenile: 6–18 months. (3) Sub-adult: 18 months to 4 years. (4) Adult: >4 years (Caister et al., 2003; Le Pendu and Ciofolo, 1999) based on giraffe body size, color, and the shapes of the ossicones. We were able to identify each individual by their unique pelage pattern. In total, 65 individuals (28 adult males, 20 adult females, 10 sub-adult males, 3 sub-adult females, 2 juveniles and 2 calves) were identified in 2017. Two female–calf dyads (dyad 1 as F1 and C1, dyad 2 as F2 and C2) and one female–juvenile dyad (dyad 3 as F3 and J3) were identified during our observations. Female–filial offspring dyads are referred to using their respective numerical identifier in the text and tables. In fact, we conducted our field study in 2010, 2011 and 2016, and these three females were monitored since 2010. They had been observed with their offspring in previous study periods; F1 was observed with a juvenile in 2016 and F2 and F3 were each observed with a calf in 2010. These three female-offspring dyads in 2017 often formed a nursery group, and no other female-offspring dyad was found in this nursery group. Sometimes another individual was found in the area where the nursery group was present, but after few hours they usually moved away and got separated from the nursery group. However, there was an exception that F1 was followed by a particular male giraffe (named M1) for almost all the time, and they were observed in the same herd for 28 out of 29 observational days of F1. Their mating was observed on October 24 and November 7, respectively.

Since we also conducted another study from June through November 2016 and from May through September 2017, we could estimate the birthdate of the three offspring in the dyads. To estimate the offspring birthdate, we used the time between the last date when a female was observed without her offspring and the first date she appeared with her offspring: for C1, 19–24 August; for C2, 5–20 July; for C3: 12–28 August 2016. Therefore, the estimated ages of the three offspring when we conducted our study of suckling and allosuckling (i.e., October through November 2017) were as follows: C1, 2–3 months; C2, 3.5–4.5 months; J3, 14–15 months. Weaning may cease before reaching 1 year of age, but sometimes suckling may continue for up to 1.5–2 years (Dagg and Foster, 1976; Langman, 1977). In addition, females are known to become pregnant while nursing (Nakamichi et al., 2015).

As Pratt and Anderson (1979) reported, giraffe calves and juvenile stay close to each other. Once located, we conducted a focal animal sampling of the offspring (Altmann, 1974). The duration of observations (hours) of all dyads were shown in Table 1. We were able to find the three offspring almost every research day (i.e., C1 and J3 for 29 days, C2 for 28 out of 32 research days). The maximum continuous observation time of a single session was approximately 4 h. We defined a suckling bout (successful suckling/allosuckling) as when the offspring took the female's nipple into its mouth and suckled for at least 5 s. A suckling attempt (unsuccessful suckling/allosuckling) was defined as when the female starts to move away before the offspring could reach the female's nipple with its mouth or when she starts to move away within 5 s of initiating the suckling by the offspring. An interaction event included both bouts and attempts. In our observations, we recorded the following data when they occurred: all suckling/allosuckling interactions, their success or failure, duration of a suckling bout, the initiator (suckler or female; female approaches the offspring to within 3 m, waits till the offspring comes close to her, and sniffs the offspring or female approaches and sniffs the offspring), identity of the nursing female, and the terminator of the suckling bout (suckler, female, or others).

Table 1

Observation hours for each dyad (upper row of each dyad) with the number of all suckling/allosuckling interactions, the number of successful suckling/allosuckling in brackets. The female–filial offspring dyads are indicated by a gray background, and successful allosuckling bouts were underlined.

	C1	C2	J3
F1	116	108	104
	55 (37)	1 (1)	34 (4)
F2	108	112	104
	5 (0)	63 (14)	35 (0)
F3	104	104	104
	0 (0)	1 (0)	34 (5)

The Steel–Dwass test was used for post hoc comparisons of suckling duration among the three offspring. This test was chosen because Kruskal–Wallis test was significant for suckling duration among the three offspring (df = 2, $p < 0.05$). Ryan's test for multiple comparisons was performed to assess the differences in (1) the rate of suckling bouts per suckling interaction among the three offspring, (2) the number of allosuckling interactions per observation time among the three offspring. Fisher's exact test was used to examine the combination of two suckling conditions (bouts or attempts) in relation to the combination of the initiator. A G–test with the William's correction was used to test for deviation from random occurrence of a terminator of suckling bouts among each category. We report the mean ± SE in the text. All statistical calculations were performed using the R statistical package (R Core Team, 2016), with a two-tailed significance level set at 0.05.

With respect to suckling interactions, we observed 56 suckling bouts and 96 suckling attempts. Suckling durations of the three offspring were on average as follows: C1, 18 ± 3 s (n = 37, min: 4 s, max: 90 s); C2, 22 ± 5 s (n = 14, min: 5 s, max: 72 s); and J3, 40 ± 5 s (n = 5, min: 26 s, max: 51 s), and C1 suckled for a significantly shorter duration when compared with J3 (Steel-Dwass test: C1 vs C2, $t = 0.92$, $p = 0.63$; C1 vs J3, $t = 2.82$, $p < 0.05$; C2 vs J3, $t = 2.09$, $p = 0.09$). Table 1 summarizes the frequency of suckling/allosuckling interactions per hour for each offspring. Rate of suckling bouts per suckling interaction was significantly higher in C1 than in the other two (C1: 68%, C2: 23%, J3: 15%; Ryan's test: C1 vs C2: $\alpha = 0.03$, $p < 0.05$; C1 vs J3: $\alpha = 0.02$, $p < 0.05$). The females initiated significantly more often suckling bouts than suckling attempts (Fig. 1a. Fisher's exact test: C1: $p = 0.05$; C2: $p < 0.01$; J3: $p = 0.01$). Additionally, even though the females approached their filial offspring, other individuals, i.e. M1 and J3, approached the suckling pair before the filial offspring started to suckle, and the suckling failed. This was the main reason why the suckling interactions initiated by females ended up as an attempt at a high rate. The suckling bouts of calves were significantly more often terminated by others than by the females or the sucklers (Fig. 1b. G-test: C1: $G = 45.1$, df = 2, $p < 0.01$, C2: $G = 8.6$, df = 2, $p < 0.01$). Female 1 was never observed to terminate a suckling bout. Female 2 terminated 1 suckling bout after a duration of 72 s. The suckling bouts of J3 were terminated only by female 3.

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